# Biological Succession in the Aleutians[1]

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WORLD WAR II provided "shock treatment" to American interest in the Aleutian Islands. Prior to 1942, the Aleutians were only vaguely known, and thought of, if at all, as cold, desolate, and totally inhospitable. This ignorance was shared by scientists, military leaders, and, too frequently, by governmental agents responsible for the administration of that part of the Alaskan Territory. A sudden awakening came when the United States and Canada were forced by the exigency of war to land and maintain a large force of men on these hitherto neglected shores, and immediately they assumed new importance as our North Pacific frontier. Attesting to this new importance is the fact that eight university-sponsored expeditions have been sent to explore the islands in the past 4 years. Greatly outnumbering these have been governmental survey parties and individual investigators. In all, more than 30 scientific projects have been directly concerned with the Aleutian Chain in postwar years. Moreover, this surge of interest seems likely to continue, as several current programs are organized on a long-term basis.

Wartime and early postwar studies were naturally concerned more with the strategic potentialities of the islands for military occupation than with purely scientific questions. However, from these investigations have come an increasing appreciation of the peculiar ecological relationship which exists between Aleutian environment and biota. Here a unique set of environmental factors has molded flora, fauna, and human culture into patterns quite different from those on most of the Mainland. This paper will outline briefly some of these patterns, which are transitional stages of biological succession.

Field work upon which this paper is based has been sponsored by the University of Michigan, the Michigan Phoenix Project, and the Office of Naval Research. In all, four trips have been made to the Aleutians, during which more than 20 islands were visited. Critically important localities such as glacial margins, hot springs, volcanic craters, and prehistoric village sites were given special attention by members of our expeditions, and an attempt was made to correlate biological and anthropological investigations with a view toward establishing a chronology of postglacial events in the Aleutians.

## PLEISTOCENE PHYTOGEOGRAPHY

The most ambitious phytogeographical treatment of arctic and subartic regions in Pleistocene times is that of Dr. Eric Hultén (1937*b*). For reviews of his hypotheses, the interested reader is referred to several excellent summaries which have been published (Raup, 1941, 1947; Cain, 1944). It will be useful, however, to outline quickly Hultén's major conclusions regarding the Aleutians.

Hultén undertook extensive field work in both Kamchatka and the Aleutians, supplementing this with an examination of all available herbarium material from the arctic and

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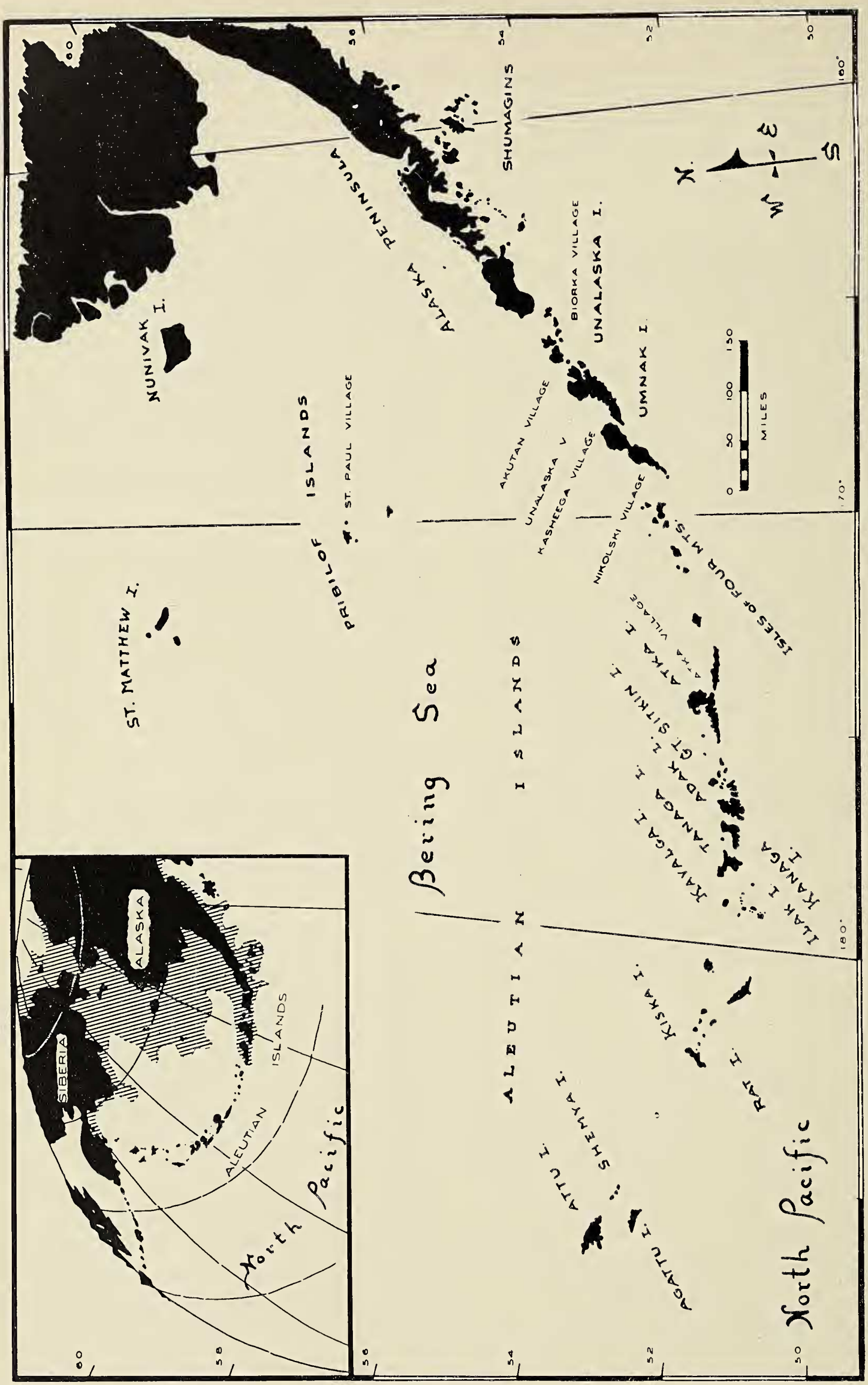


FIG. 1. The Aleutian Islands. Probable extent of ancient "Beringia" is indicated by diagonal hatching in insert.

boreal regions. Natural ranges of hundreds of plants were mapped. Ranges which were more or less congruous were grouped. Each group was thus made up of superimposed ranges which were approximately equiformal and of progressively larger area. Hultén termed these "equiformal progressive areas." He showed that each such area has a center, i.e., a region where the largest number of biotypes occurs. This is presumed to be the center of origin, and from here the plants dispersed to occupy their present ranges. Those with ranges that approximate closest the center are termed "centrants" and those with wider ranges are termed "radiants." Geographically, the centers all lie outside the maximum advance of the ice sheets and thus probably served as the major plant refuges during Pleistocene glaciation. Some plants which survived in the more extensive refugia retained their genetical ability to reproduce and quickly occupy new ice-free areas following the glacial periods. Others, on more isolated, smaller refugia, became depauperated of biotypes with the result that their spreading ability was reduced. Hultén has termed them "rigid" species. The quickly spreading plants are termed "plastic" species.

One of the most important plant refuges was an ice-free lowland which Hultén has called "Beringia," a land area thought to have existed at various times during and immediately following the Pleistocene when sufficient water was withdrawn from the ocean to expose much of the sea floor in the northern and eastern Bering Sea and southern Arctic Ocean regions (Fig. 1). From Beringia, from unglaciated portions of the eastern Aleutians and extensive ice-free areas in Kamchatka, biota surviving the pleistocene are presumed to have spread to adjacent areas as the ice withdrew. The most highly plastic species were the first to re-establish themselves on such places as the central Aleutians, which Hultén thinks were heavily glaciated and hence mostly devoid of plant life during the glacial periods. Through such differential migrations of plants from both ends of the Aleutian Arc due to unequal spreading of plastic and rigid species, the present Aleutian flora came into being. Thus, the characteristic middle-Aleutian gap which occurs in the distribution of many species (Hultén, 1937*a:* 348–381) is the result of the inability of rigid types to invade the islands as quickly as plastic ones.

Hultén's methods of arranging the equiformal progressive areas are open to certain criticisms (Raup, 1947: 231): (1) additions to his lists are undoubtedly forthcoming and may alter some equiformal areas; (2) many of the gaps in plant distribution can be shown to be gaps in exploration; and (3) Hultén's sorting of species to illustrate equiformal areas may represent a faulty technique. However, such criticism is comparatively minor, and none of the recent work has seriously altered Hultén's general hypothesis.

An example of the second criticism of Hultén's work is found in our own studies. We are now able to fill in many gaps of distribution of Aleutian plants. *Eriophorum russeolum*, for example, was supposed by Hultén not to occur between Umnak in the eastern Aleutians and Kamchatka, but we have since found it on Atka, Adak, Kiska, and Attu (Fig. 1). Likewise, *Prunella vulgaris* var. *aleutica* occurs on several islands of the middle Aleutians, where it was supposedly absent. Thus, of 105 species which theoretically have had distributional gaps in the middle Aleutians, 24 have been found on islands within the gaps. It seems likely that more will turn up as further exploration covers additional ground.

Such new and important range extensions indicate that much additional field exploration is needed. Hultén's supposition that the middle islands were heavily glaciated during the Pleistocene is not entirely correct, because subsequent work has indicated that a number of ice-free islands probably existed (U.S.G.S., 1947): for example, west of Adak, the flat, platform islands of Ogliugla, Ilak, Kavalga,

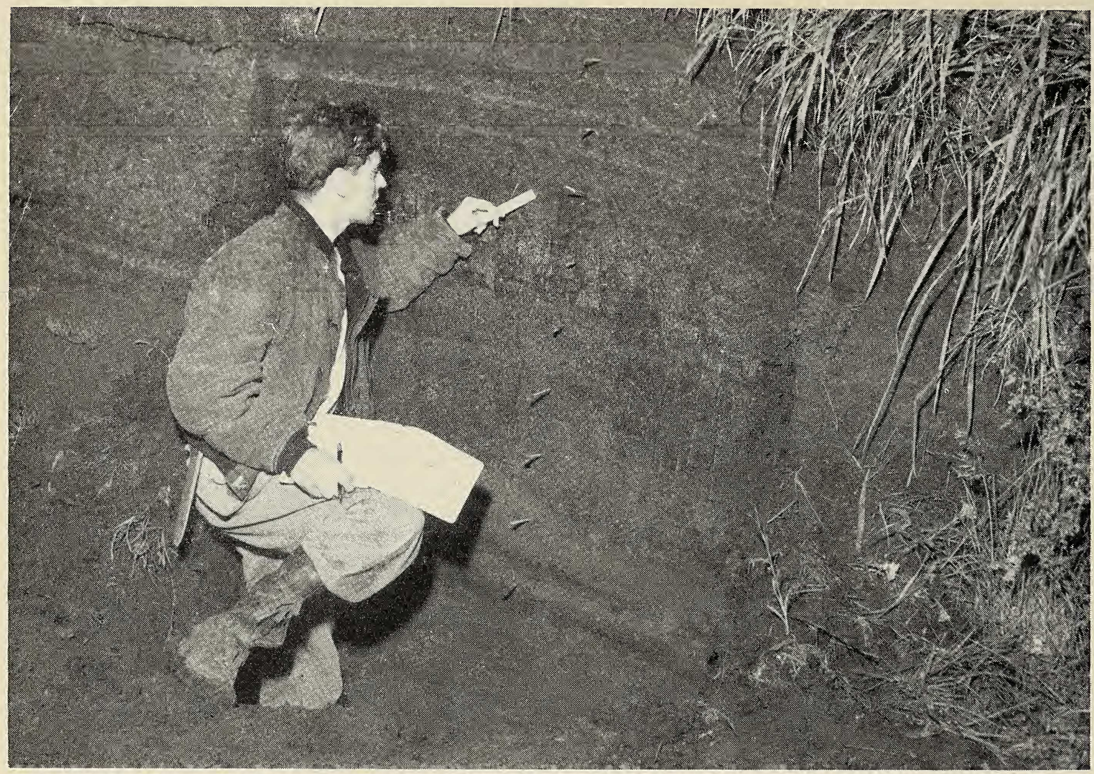

FIG. 2. Newly exposed postglacial ash profile on Tanaga Island, August, 1950. Ash, humus, and clay strata are clearly defined.

Unalaga, and Shemya, and parts of Kanaga, Tanaga, etc. These undoubtedly served as refugia for a number of hardy plants which were able to withstand the climatic rigors and the proximity of nearby ice caps on Adak, the northern parts of Kanaga and Tanaga, Amchitka, and Semisopochnoi.

### POSTGLACIAL PLANT SUCCESSION

The ecological concept of succession is hard to apply to communities which continually fluctuate in an unstable way so that a so-called climax grouping today may be shown later to have been only temporary. Under such conditions, succession is difficult indeed to define and more difficult to understand, especially if brief field studies attempt to name characteristic or dominant species as criteria of certain stages. In the Aleutians what one thinks of as a successional stage or climax community is often found to consist of characteristic species which occur widely in other habitats and make up a large part of the local flora. Moreover, the community may be replaced by another during a relatively short period of time only to reappear again in slightly different form. Hultén has called attention to this by remarking (1937*a*) that the Aleutian plant associations are very similar to those of Kamchatka, but in the Aleutians the associations are much less stable. There is considerable shift back and forth in species within communities, which results in the dropping out of various members. There are also abrupt shifts in entire plant communities which result in a radically new vegetative character of a comparatively large area.

In postglacial times, as Aleutian plant life reinvaded the newly ice-free areas from various refugia, there undoubtedly occurred major disruptive phenomena which seriously interfered with normal plant succession. During volcanic eruptions, for instance, large areas were completely covered by ash, and the vegetation was thus exterminated. Major ash falls are clearly marked in the soil profiles (Fig. 2). A number of such ash falls must have originated from violent eruptions which gradually diminished to a rather continuous, comparatively quiet eruption of long duration. The results of this activity appear in the profile as layers composed of coarse pumice overlaid by ash which becomes increasingly finer toward the top. These deposits are often 0.5 meters or more thick and are almost pure volcanic material devoid of any organic remains. Frequently they separate layers of almost pure humus (Fig. 3). The vegetation was destroyed by the ash fall and had to reinvade the area, in time producing the overlying humus. Thus, it is somewhat possible in the Aleutians to follow both the volcanic history and the major accompanying disruptions in plant succession.

Pollen studies of humus intercalated between ash strata offer one method of arriving at a history of postglacial plant succession, and for this purpose hundreds of soil samples were secured from various ash profiles and archaeological sites. Several of these samples have already been examined briefly for pollen by S. T. Anderson, and a preliminary report of the results has been released (Anderson and Bank, 1952). These are interesting and worth summarizing. Two humus samples from soil strata, one at 0.92 meters depth and the other at 1.83 meters depth, came from a single ash profile on Tanaga Island in the middle Aleutians. Usually, terrestrial ash-soil deposits should not contain much pollen, as the grains would ordinarily be destroyed by oxidation. It was therefore somewhat surprising to find that these samples contained sufficient pollen for quantitive studies. This is probably because of the unusual Aleutian climate, marked by consistently high precipitation and fairly low soil temperatures. Many Aleutian soils are constantly saturated with water, which undoubtedly is a major factor in the preservation of pollen and spores.

The samples were treated according to the procedure described by Faegri and Iversen (1950). Pollen from the lower part of the profile represents an entirely different plant community from that of the upper part. The

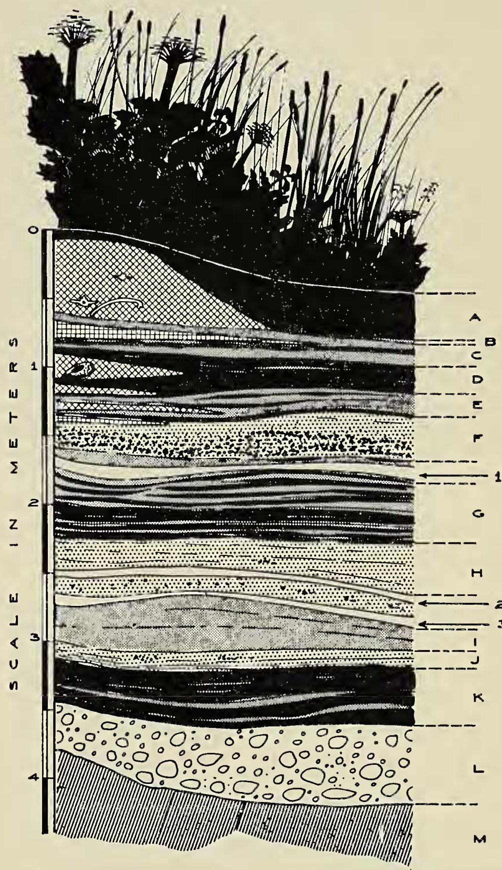


FIG. 3. Diagrammatic profile at the edge of an Aleut kitchen midden on Nazan Bay, Atka Island. Vertical and diagonal cross-hatching indicates clam shell, fish bone, and sea urchin shell deposits (archaeological). Also shown are sea lion bones and a stone lamp in position. The nonarchaeological strata are: A, recent humus; B, sand; C,E,I, fine ash, slightly stratified; D,G,K, humus with fine ash admixture, stratified; F, H,J, coarse pumiceous ash; L, brown clay with large pumice (till ?); M, bedrock; 1,2,3, ferruginous bands (from leaching from above?). Surface vegetation, especially lush on such sites, is indicated and includes: *Heracleum lanatum*, *Elymus arenarius* subsp. *mollis*, *Conioselinum Gmelini*, *Angelica lucida*, *Aconitum maximum*, *Claytonia sibirica*, *Achillea borealis*, and *Calamagrostis canadensis* var. *Langsdorffii*.

older pollen and spores consist of high percentages of *Ericales* (55 per cent), Gramineae (22), and *Lycopodium* (17), with some Cyperaceae (2.9). Thus, the lower sample represents the *Empetrum* heath of higher altitudes (Hultén, 1937*a;* Bank, 1952). The younger pollen and spores show high percentages of Gramineae (56), Cyperaceae (23), and Ranunculaceae (9.0), with some *Ericales* (3.7), *Dryopteris* (3.1), and Umbelliferae (2.2). This sample indicates a vegetation very similar to the *Calamagrostis* meadow which exists today at the place of the profile.

The results of this preliminary pollen study are, of course, inconclusive. What they do indicate is that pollen analysis of at least some strata in Aleutian ash profiles is possible. Certain changes in vegetation are indicated, i.e., from an earlier *Lycopodium-Empetrum* heath to a *Calamagrostis*-Umbelliferae meadow, and these changes can be interpreted as due to climatic fluctuation from dry, continental-arctic to moist, oceanic-subarctic. However, great dependence upon pollen shifts at isolated sites as an indication of widespread climatic changes is extremely hazardous for two main reasons: (1) it seems likely that heavy ash falls not only destroyed existing vegetation but also produced such radical changes in the local habitat that the succeeding vegetation may have been of totally different character for edaphic reasons; and (2) the normal instability of Aleutian biota, to which I have already called attention, operates to produce major changes in natural biotic groupings for reasons much less basic than climatic interference.

Raup (1950) has discussed this latter general problem of physiographic ecology in arctic and subarctic regions. He says (p. 8): "Approaches to equilibrium or relative stability such as we find in the temperate regions and are wont to call climax, are almost impossible to define in the Arctic and much of the Subarctic. At best they are ephemeral in time and space." And again (p. 10), ". . . it becomes apparent that one of the prime requisites for development of dominance and succession—long continued stability in the substratum—is absent or very poorly represented over vast areas in the Arctic and Subarctic."

An example of a constantly unstable substratum in the Aleutians is found in the alpine regions where the unceasing wind, more than any other ecological factor, restricts plant growth, molds vegetational structure so to speak, and, when aided by subsurface water, often radically changes the vegetational character of large areas in a comparatively short period of time. Thus in high, exposed places one frequently comes upon bare patches of gravel or ashy soil having a slight ridge along the lower margin. These areas are wet and are usually on slopes. Underground seepage has saturated the soil, which lies thinly over bedrock, with the result that large soil patches have flowed downhill carrying vegetation with them. Surface water further erodes these areas, and wind removes all loose plant fragments. The bare patches may be reinvaded by plants, but irregular shallow depressions in the surface of the vegetational mat identify the spot as a former slough area. Frequently these are continually eroded by the high winds, and scalloped gravel pits are formed. The gravel-blasting effect of the wind prohibits all but the hardiest plants from gaining a foothold. At first only gnarled, almost leafless, dwarfed (6 inches tall) willows may grow. In time these eroded patches are probably covered by willows and lichens, which in turn offer some protection from the wind to less hardy plants, among them *Campanula lasiocarpa*, *Primula cuneifolia*, *Antennaria dioica*, and *Polygonum viviparum*.

Probably the best examples of vegetational instability are found in the wet habitats. Often these develop in the middle of an otherwise dry Aleutian meadow or heath area. In such places subsurface water may begin to seep from the hillside and form bog-like drainage slopes on which a number of bog plants, especially *Sphagnum*, begin to grow. Soon

FIG. 4. Temporary bog in the middle of a lowland meadow, Atka Island. Seepage from surrounding hillsides collects here, and plants typical of wet habitats invade the area. These plants include: *Carex Lynghyaei* and other *Carex* spp., *Plantago macrocarpa*, *Polygonum viviparum*, *Platanthera dilatata*, *Juncus balticus*, *Erigeron perigrinus*, *Eriophorum Chamissonis*, etc.

these areas are inhabited by liverworts, *Sphagnum capillaceum*, *S. Girgensohnii* and other mosses, *Saxifraga punctata* subsp. *insularis*, *Leptarrhena pyrolifolia*, *Viola Langsdorffii*, *Pinguicula vulgaris*, sometimes *Scirpus* spp., and *Carex* spp. Their growth often becomes extensive and deep enough to necessitate a wide detour when walking across a hillside. These are usually temporary features, however, and such wet places, with their typical vegetation, constantly appear and disappear under the influence of fluctuating subsurface drainage patterns, which are in turn greatly affected by yearly variations in snow accumulation. True peat bogs, such as those common to parts of mainland Alaska and Canada, are not found in the Aleutians. Instead the bogs are of the type just described, formed from seepage, or are essentially low areas containing water-saturated mud overlaid by scattered growths of sedges, *Juncus* spp., short grasses, and sometimes *Sphagnum* (Fig. 4). Usually such areas are shallow, but some are deep enough to completely mire large vehicles. Many such mud bogs are only a transitional stage for shallow ponds and meadows. I observed an amazingly quick replacement of *Carex Lyngbyei* and *Eriophorum Chamissonis* by *Calamagrostis canadensis* var. *Langsdorffii* and other grasses after one such bog was drained by military operations.

Other evidences of instability are noticeable in stream ravines. Usually occurring here are ferns (*Athyrium Filix-femina* and *Dryopteris* spp.), grasses such as *Deschampsia beringensis*, mosses, *Streptopus amplexifolius*, *Epilobium angustifolium* var. *macrophyllum*, frequently *Artemisia unalaskensis*, and various umbellifers. The profuse vegetation frequently grows out over the stream and in time may entirely cover

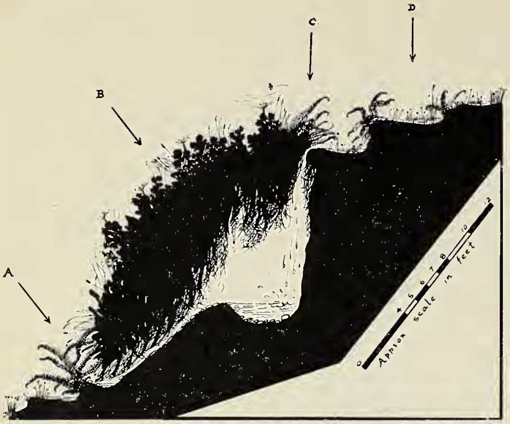


FIG. 5. Diagrammatic profile of part of a typical "slumped" stream bed and underground channel. Such stream tunnels, A–C, are fairly common in the Aleutians and can be dangerous should a person fall through the ceiling B. The lower outlet A and the upper entrance C are usually choked with ferns and other plant growth. The tunnel ceiling usually possesses a meadow vegetation, consisting of grasses, umbellifers, *Streptopus*, *Claytonia*, etc. At D a series of terraces are formed from a former tunnel ceiling which slumped gradually and finally caved in. The vegetation here is usually bog-like, with *Sphagnum*, *Carex*, *Juncus*, liverworts, and *Saxifraga* predominating.

the ditch so that the stream flows through an underground tunnel (Fig. 5). These places can be quite dangerous. Hultén (1937*a*) mentions falling through the ceiling of one such tunnel. Hidden streams may persist this way for a considerable time, but usually the overhanging mat is penetrated by surface drainage, holes reappear, the overhanging mat slumps, and the ditch becomes a series of depressions or wet terraces composed of sphagnum and typical bog plants, a much different vegetation than that which formerly occurred in the ravine.

In the Aleutians, this instability of substratum and plant cover does not have precisely the same causes as on the mainland. Permanent subsurface ice (permafrost), for example, is not the very important factor that it is over widespread areas of Siberia, mainland Alaska, and Canada. Rather, instability is probably a result of the interaction of the edaphic and climatic factors which make the Aleutians more or less unique: namely, a comparatively thin soil mantle largely of volcanic ash, more or less continuous ash deposition, temperate conditions with heavy precipitation, cool summers, and unusually high, rather constant winds.

Kellogg and Nygard (1951) have characterized the Aleutian substratum as "tundra without permafrost" and composed of silty or sandy loam with ash. There are, however, small areas of permanent subsurface ice in the Aleutians which may be fairly extensive albeit sporadic and seemingly of little influence on surface vegetation. I observed one such area on Great Sitkin Island where Glacier Creek has cut through an ancient mud flow. Ice is exposed in the profile about 20–30 feet below the surface of the old flow. Thick sheets and occasional lenses of ice can be traced along the floor of the stream bed for distances of 25 to 50 yards. Strictly speaking this is not permafrost but relict glacial ice. The surface topography and vegetation are unmodified, and it is presumed that the depth at which the ice occurs is too great to affect plant growth above. Melting of the ice masses, however, will undoubtedly cause local land slumps leading to the formation of kettles and, thus, different microhabitats which will have their peculiar plant communities.

## RECENT PLANT INVASIONS

The foregoing examples of fluctuating vegetation in the Aleutians illustrate the spreading ability, i.e., plasticity, of some plants of this area. This ability has been noted by Hultén (1937*b*) who writes that on Bogoslof, the "jack-in-the-box" island that has appeared and disappeared a number of times in the last 150 years, a pioneering vegetation is already well established. It includes *Lathyrus maritimus*, *Elymus arenarius* subsp. *mollis*, *Honckenya peploides major*, *Puccinellia pumila*, and *Mertensia maritima*, all of which are widespread littoral plants. *Senecio pseudo-arnica* also occurs on the still-warm shores. Our own field parties studied briefly several pioneer plant communities near a small glacier on the upper slopes of Great Sitkin Island (Fig. 1). We visited the place on two occasions 12 months apart. It was noted in 1950 that during the preceding year a considerable extent of newly ice-free area had been successfully invaded by a number of plants, mostly mosses and lichens but also including *Luzula arcuata*, *Agrostis exarata*, *Hieracium triste*, *Carex circinata*, and *Sibbaldia procumbens*. Although the actual creep of vegetation was in most cases only a few feet, this was all along the margin of the newly exposed ash, a sizeable area, and seems remarkable for having occurred during a single growing season.

Contrasting with this is the inability of *Picea* to establish itself on Aleutian soil, despite the fact that extensive spruce forests occur on the mainlands of Alaska and Kamchatka at the same latitudes. On Amaknak Island in Unalaska Bay in 1805 Russian settlers planted 24 seedlings of *Picea sitchensis* which came from Sitka (Hultén, 1937*a*). Other Sitka spruces were later planted on Expedition Isle in Roose Bay and in Unalaska Village. All these groves have been depleted by dying trees, but parts of the original plants are still alive, and, except for the stunted appearance and gnarled form of some of the trees, they seem healthy. Many regularly produce cones. However, none has successfully reproduced by seedlings. More recently, at Adak, several dozen Sitka spruces were planted on a hill and on a lowland. These plantings are failures; the trees that have survived are stunted, and there has been no reproduction.

Such lack of success on the part of the spruce in taking hold in the Aleutians has been attributed to various causes, among which the acid soil conditions, high winds, and constant fog are most often given. None of these answers satisfactorily explains the real reasons why the trees fail to grow in the Aleutians, however. The so-called extreme acidity of Aleutian soils is probably a misconception (Kellogg and Nygard (1951) have found that soil *p*H in the Aleutians is about the same as that on Kodiak where there are spruce forests), many of the planted groves are fairly well sheltered from the winds, and it is difficult to see how fog could prohibit tree growth entirely. I can only guess at the true reasons, as the proper studies have not been made. It is suggested that the primary ecological factor operating against spruce regeneration is the absence of any prolonged summer period of uniformly high enough temperatures to allow maturation of seed.

## CULTURAL SUCCESSION

Turning from a discussion of the effects of Aleutian environment upon biological succession to a brief consideration of the ways in which human culture has been conditioned by the same environment, we find that the Aleut was confined to a rather restricted range of cultural adaptations, which depended upon the sea and the shore. The Aleut seldom visited the inland regions of his islands, partly because topography and weather factors in those parts made such journeys a hardship, but mainly because the majority of his needs were found only on the shore, in the lowland meadows, valleys, and marshes near the sea, or in the sea (Bank, 1952). Of more than 50 local plants which the Aleut gathered for food, drink, medicines, and for use in the manufacture of such articles as grass mats, baskets, bidarki (kyak) frames, etc., almost all occurred along the margins of the islands. The Aleut depended upon fish, sea mammals, shell fish, and birds for food, and these also came from the sea or near the shore. Thus, even if Aleut culture had not been predominately maritime prior to its arrival in the Aleutians, it certainly was unable to be anything else after the Aleut took up his habitation in the Archipelago. Recent archaeological studies (Jochelson, 1925; Laughlin, 1951) have shown that Aleut culture changed only slightly during 3,000 years of occupation in the islands before the coming of the white man.

Early Russian accounts (Jochelson, 1925: 23) suggest that Aleut villages were on exposed points of land and isthmuses prior to

1741. This was because survival of an attack of a stronger warring party required access to an escape route by sea on more than one side. After the Russians had put an end to inter-island warfare, the villages were supposedly moved to sheltered bays which offered many advantages of improved fishing and better harbors. This view is somewhat substantiated by vegetational patterns, for old villages located on points of land (thus presumably pre-Russian) usually possess a comparatively less dense plant cover than do old villages located in bays. The latter sites (presumably more recently abandoned) often have a particularly lush plant cover.

However, an outright assumption that the oldest sites are to be found on points of land or isthmuses along the coasts should not be made. It is known that the islands have been rising throughout the history of the Archipelago. Jaggar (1908: 32) mentions finding old beach terraces on Unalaska at 130 meters altitude. Veniaminof (Petrof, 1884: 148) and Hultén (1937*a:* 24) also call attention to old shore lines, and more recently they have been reported by members of the U. S. Geological Survey field parties (U.S.G.S., 1947: 102). These places have not been explored archaeologically, although Hrdlička (1945) mentions several village sites in the eastern part of Agattu at a considerable distance above the sea, and I have also noted from the air an old village situated on a cliff high above the sea in the western part. It is entirely possible that future reconnaissance will uncover the oldest sites on such uplifted beaches, and it may be that here is where the true beginning of Aleut culture will have to be sought.

## SUMMARY

Study of biotic patterns in the Aleutians shows them to be extremely unstable. There are frequent vegetational shifts which results in a totally new plant cover over comparatively large areas. In postglacial times some of these shifts may have been caused by climatic changes, but it is believed that most of them have come about through unstable soil conditions, which in turn have been influenced by fluctuations in seasonal weather. Wind is a very important factor determining vegetational structure and composition ar higher altitudes. Any semblance of normat plant succession as it is known in similal latitudes on the mainlands of Asia and America is frequently altered by the combined effects of volcanic ash eruptions, wind erosion, periodic moisture surpluses (after heavier-than-usual winter snowfalls), etc. In general, vegetation is much less stable and biological succession more erratic in the Aleutians then on the mainlands. This is in sharp contrast to Aleut culture, which apparently remained unchanged in most of its major aspects during 3,000 years of existence in the Aleutians.

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